

A von Bertalanffy Growth Mode! with a Seasonally Varying Coefficient

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CLOERN, J. E., AND F. H. NICHOLS. 1978. A von Bertalanffy growth model with a seasonally varying coefficient. *J. Fish. Res. Board Can.* 35: 1479-1482.

The von Bertalanffy model of body growth is inappropriate for organisms whose growth is restricted to a seasonal period because it assumes that growth rate is invariant with time. Incorporation of a time-varying coefficient significantly improves the capability of the von Bertalanffy equation to describe changing body size of both the bivalve mollusc *Macoma balthica* in San Francisco Bay and the flathead sole, *Hippoglossoides elassodon*, in Washington state. This simple modification of the von Bertalanffy model should offer improved predictions of body growth for a variety of other aquatic animals.

Key words: Bertalanffy, growth model, growth rate, *Macoma balthica*

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Le modèle de croissance corporelle de von Bertalanffy ne peut s'appliquer à des organismes dont la croissance se limite à des périodes saisonnières, car il suppose que le rythme de croissance ne varie pas avec le temps. Si l'on incorpore à l'équation de von Bertalanffy un coefficient variant avec le temps, elle décrit beaucoup mieux la taille changeante, à la fois du mollusque bivalve *Macoma balthica* dans la baie de San Francisco et de la sole à tête plate *Hippoglossoides elassodon* dans l'Etat de Washington. On devrait pouvoir se servir avec profit de cette simple modification du modèle de von Bertalanffy pour mieux prédire la croissance corporelle d'une variété d'autres animaux aquatiques.

Received April 28, 1978

Accepted August 1, 1978

Reçu le 28 avril 1978

Accepté le 1 août 1978

THE following function (from von Bertalanffy 1938) is widely used to describe growth of a variety of animals:

$$(1) \quad L(t) = L_{\max} - (L_{\max} - L_{\min}) \cdot \exp[-b \cdot (t - t_0)],$$

where L is length at time t ($t = 0$ on January 1), L_{\max} is a maximum body size, L_{\min} is body size at time of recruitment (t_0), and b is a constant coefficient. This relation implies that growth rate is a constant function of body size alone. While this assumption may hold for animals in a constant environment, it fails to hold for the many animals whose growth rates vary seasonally.

This paper describes a simple extension of the von Bertalanffy model that allows growth rate to vary with changing body size and with periodic (seasonal) changes in growth characteristics.

Model derivation — We assume here that the following conditions characterize the general change in body size of a given organism:

1. At time of recruitment ($t = t_0$), body size is some constant minimum (L_{\min}). 2. Growth rate is maximal ($dL/dt = L'_{\max}$) when body size is minimal. 3. There

is a constant upper limit (L_{∞}) to body size. 4. Growth rate is a (decreasing) linear function of body size:

$$(2) \quad \frac{dL}{dt} = L'_{\max} - b \cdot (L - L_{\min}).$$

Assumptions (3) and (4) are not strictly valid because many organisms exhibit indeterminate growth and because the relationship between growth rate and body size may become nonlinear as body size approaches the assumed L_{\max} (F. H. Nichols unpublished data).

However, all four assumptions are reasonable approximations that allow for simple models of the complex growth process.

Note that the solution to equation (2) is the von Bertalanffy model (equation 1). If seasonal variations in growth rate are manifested as seasonal changes in the coefficient b , then any function that describes the temporal variation in b can be substituted into equation (2), giving a differential equation that incorporates effects of both time (season) and body size on rate of growth. Its solution should give an improved description of changing body size for those animals exhibiting seasonal growth.

Nichols' study (unpublished data) of the bivalve *Macoma balthica* demonstrated that the coefficient b

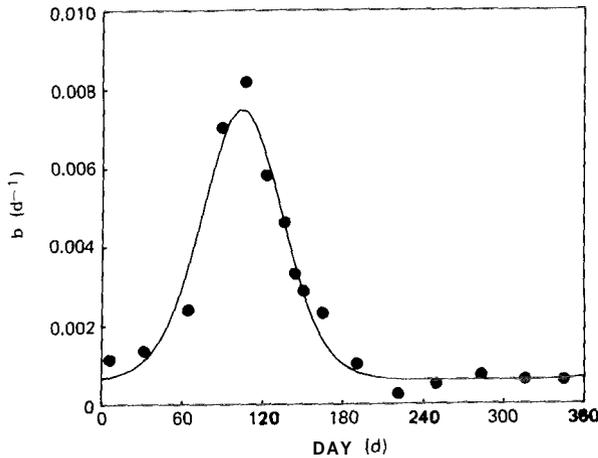


FIG. 1. Running averages of the coefficient b describing the relationship between growth rate and body size of *Macoma balthica* in San Francisco Bay. Also shown (solid line) is the fitted function given by equation (3).

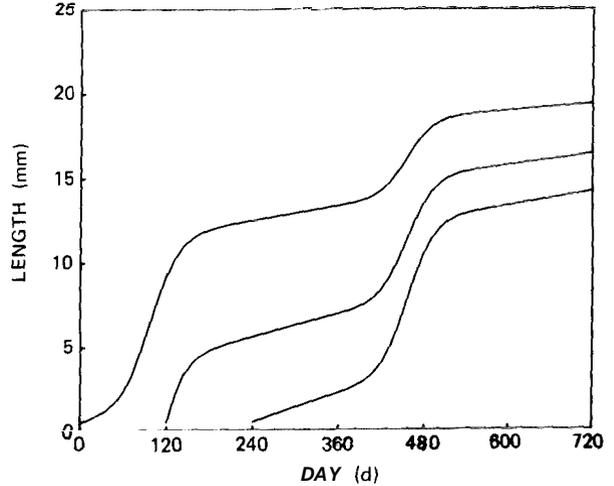


FIG. 2. Predicted growth of *M. balthica* in San Francisco Bay for three different recruitment dates ($t_0 = 0, 120,$ and 240 d).

changes over an annual cycle in San Francisco Bay. He measured growth increments of individuals from a variety of size-classes and estimated b from the slope of the linear regression relating growth rate ($\Delta L/\Delta t$ over periods of 1–3 mo) to mean body size. We have fit these estimates of b , by least squares (Powell 1968), to an empirical function of time (Fig. 1):

$$(3) \quad b(t) = a_1 + a_2 \cdot \exp \left[a_3 \cdot \sin \left\{ \frac{\pi}{180} \cdot (t + \theta) \right\} \right],$$

giving $a_1 = 6.0 \times 10^{-4}$, $a_2 = 1.7 \times 10^{-4}$, $a_3 = 3.7$, $\theta = -14.4$. Incorporation of equation (3) into (2) gives a new differential equation whose solution is

$$(4) \quad L(t) = L_{\max} - (L_{\max} - L_{\min}) \cdot \exp \left[-a_1 \cdot (t - t_0) - a_2 \cdot \int_{t_0}^t \exp \left(a_3 \cdot \sin \left\{ \frac{\pi}{180} \cdot (\tau + \theta) \right\} \right) d\tau \right],$$

where the integral can be approximated with a numerical quadrature (see e.g. Hildebrand 1974).

Certainly other modifications of the von Bertalanffy equation allow for seasonality. For example, if seasonal variations in the coefficient b follow a simple periodic function,

$$(5) \quad b(t) = a_1 \cdot \left[1 + \sin \left\{ \frac{\pi}{180} \cdot (t + \theta) \right\} \right],$$

then a simplified analog to equation (4) results

$$(6) \quad L(t) = L_{\max} - (L_{\max} - L_{\min}) \cdot \exp \left[-a_1 \cdot (t - t_0) - \frac{180 \cdot a_1}{\pi} \left(\cos \left\{ \frac{\pi \cdot (t_0 + \theta)}{180} \right\} - \cos \left\{ \frac{\pi \cdot (t + \theta)}{180} \right\} \right) \right].$$

Because it has fewer parameters and is analytic, this function may prove to be of more general use than

equation (4) which requires a numerical integration. However, if growth is truly restricted to one season (e.g. Fig. 1), then the increased accuracy of equation (4) may justify its use.

Discussion — Assuming that $L_{\max} = 24.8$ mm and $L_{\min} = 0.5$ mm (F. H. Nichols unpublished data), equation (4) traces body growth of an individual *M. balthica* in San Francisco Bay for any given recruitment date (Fig. 2). The predicted pattern of body growth is strongly influenced by time of recruitment. Individuals recruited in the spring (around day 120) initially grow rapidly, while initial growth is slower in animals recruited during other times of the year. Although individuals recruited late in the year exhibit slow initial growth, they grow faster than older individuals the following spring (Fig. 2). Hence, this model (unlike the von Bertalanffy equation) describes the process referred to as "growth compensation" (Gerking 1966; Ricker 1975) or the "catching-up phenomenon" (Lammens 1967).

Equation (4) was derived to follow changing body size of an individual, but it also describes mean body size of a cohort from a mixed population of *M. balthica* more accurately than the von Bertalanffy function (Fig. 3). In this example the data represent animals that, recruited throughout the previous year (spring to autumn), constitute a single cohort in midwinter (day 30 in Fig. 3). (The poor fit between predicted and measured lengths after day 315 results from our inability to separate this cohort clearly from others after this date.)

To demonstrate a broader application of this modified von Bertalanffy model, we fit equation (4) by least squares (Powell 1968) to mean lengths of the flathead sole, *Hippoglossoides elassodon*, over a 3-yr period (data from Miller and Wellings 1971). Small deviations from

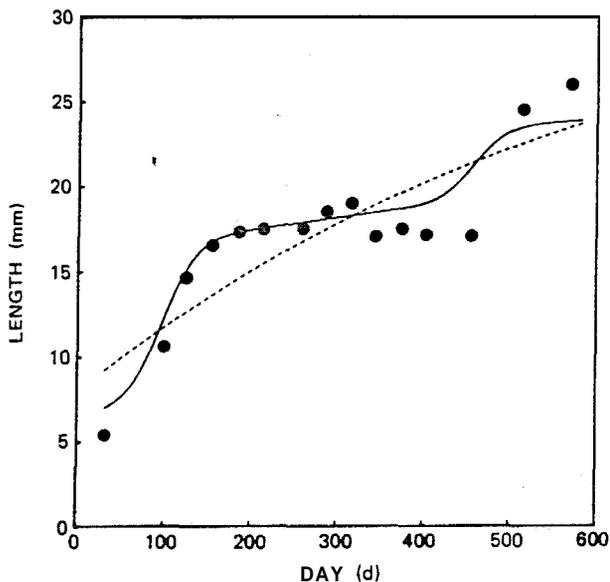


FIG. 3. Comparison of the von Bertalanffy model (equation 1, dashed line) and our seasonally varying model (equation 4, solid line) in describing mean length of a group of *M. balthica* in San Francisco Bay. In fitting measured lengths to equation (4), equation (3) was assumed and only L_{\min} and L_{\max} were estimated by least squares (Powell 1968). Data were fit directly to the von Bertalanffy model by least squares.

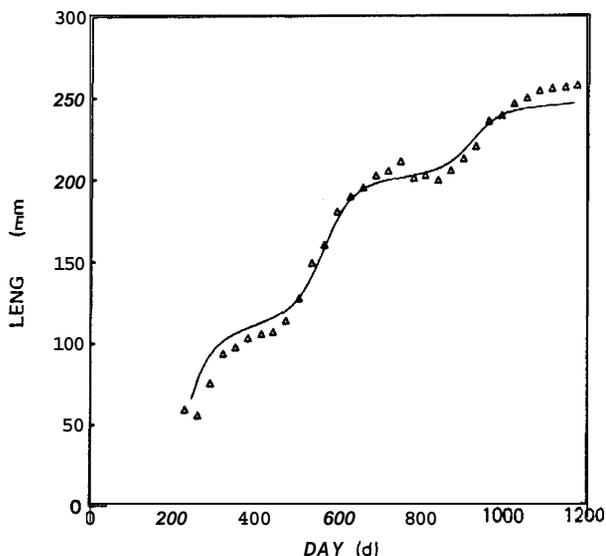


FIG. 4. Mean length of (normal male and female) *Hippoglossoides elassodon* over a 3-yr period (from Miller and Wellings 1971). Also shown (solid line) is the least-squares fit to equation (4), assuming that $t_0 = 245$.

the model do exist (Fig. 4), probably because of year-to-year environmental variations. But because equation (4) acknowledges the obvious seasonal changes in

growth rate, its prediction of body growth in the flathead sole is an improvement over the simple von Bertalanffy hyperbola.

The assumption of a constant coefficient b probably fails to hold for a number of aquatic organisms. For example, Warren and Davis (1967) demonstrated that growth efficiency of the reticulate sculpin (*Cottus perplexus*) and cutthroat trout (*Salmo clarki*) vary with season. Fortin and Magnin (1972) found that annual growth of the yellow perch (*Perca flavescens*) is restricted to a 4-mo growing season in Lake St. Louis, and Gerking (1966) reported that the length of the growing season of the bluegill sunfish (*Lepomis macrochirus*) varied among lakes in northern Indiana from 3–6 mo. The temporal changes in growth in all these species are consistent with equation (3) and suggest that our extension of the von Bertalanffy model may offer improved descriptions of body growth for a variety of animals.

Seasonal variations in the growth of aquatic animals are, at least in part, related to temporal changes in air and water temperature and seasonal variations in abundance and quality of food (e.g. for *M. balthica* see de Wilde 1975 and Beukema et al. 1977). A model that incorporates realistic assumptions about growth and predicts observed patterns of growth may prove useful in directing studies of these relationships. Moreover, the accuracy of the new model makes it useful in pointing to nongrowth processes that affect mean size in populations, such as size selective mortality and continuous or intermittent recruitment patterns.

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